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OSCILLATIONS IN ROD AND HORIZONTAL CELL MEMBRANE POTENTIAL: EVIDENCE FOR FEED-BACK TO RODS IN THE VERTEBRATE RETINA

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SUMMARY

1. Rods and horizontal cells were studied with intracellular recordings in the retina of the toad, *Bufo marinus*; 161 cells were from the eyecup preparation and thirty were from the isolated perfused retina.

2. Of these cells, 39 % exhibited either transient or sustained oscillations of membrane potential. Light flashes either evoked transient oscillations or temporarily abolished sustained oscillations. The amplitudes of the oscillations could be as large as 27 mV. The frequency of the oscillations at 25° C was between 1·5 and 3·5 Hz and was strongly dependent on temperature and background illumination.

3. The rod oscillation amplitude and the peak of the horizontal cell light response increased similarly with increasing test flash diameters. They continued to grow for diameters much larger than those which increased the peak of the rod light response.

4. Perfusion of the isolated retina with 2 mM aspartate had only a small effect on the rod light response but it completely eliminated the horizontal cell light response as well as the oscillations recorded in both rods and horizontal cells.

5. It is believed that the oscillations result from a reverberating interaction between rods and neurones post-synaptic to rods. Thus, rods can be both post- as well as presynaptic retinal elements.

INTRODUCTION

The vertebrate retina has a number of mechanisms by which signals spread laterally and influence the radial flow of information from the photoreceptors to the ganglion cells. Lateral interactions involving the tangentially oriented horizontal cells and amacrine cells have been described at the outer plexiform layer (Werblin, 1974) and at the inner

plexiform layer (Werblin & Copenhagen, 1974). Other mechanisms are provided by the arborized bipolar and ganglion cells, and by the interactions which occur between the receptors themselves (Baylor, Fuortes & O'Bryan, 1971; Schwartz, 1973). Previous studies have shown that lateral interactions in the retina which couple the radially oriented neurones can cause periodic activity at the retinal output. Oscillatory massed activity has been recorded in the visual cortex, lateral geniculate body, optic tract and in the electroretinogram (for a review, see Doty & Kimura, 1963). This oscillatory activity has been recorded in the visual systems of a large variety of animals but the mechanisms responsible for its genesis have yet to be elucidated.

Studies of oscillating activity directed at determining the site of the phenomenon have produced conflicting results. Brindley's (1956) differential depth recordings in the isolated frog retina showed maximum oscillating activity between the external limiting membrane and the outer nuclear layer. Anderson & O'Steen (1971) demonstrated the requirement of functional photoreceptors for recording oscillating behaviour. However, the recent work of Graham & Pong (1972) and Ogden (1973) suggests that the origin of the oscillations might be in the more proximal retina.

This study describes results obtained on toad retinal neurones which exhibited oscillations in membrane potential. It is shown that the green sensitive rods and horizontal cells can exhibit oscillating behaviour. The receptive field properties of these oscillating cells are explored, as is their behaviour in sodium aspartate, a chemical which has been shown to eliminate horizontal cell activity (Cervetto & MacNichol, 1972). The results suggest that toad rods can be post- as well as presynaptic neurones and can be affected by the activity of neighbouring cells.

METHODS

Adult specimens of *Bufo marinus* were used in these experiments. For the eyecup preparation, an eye was enucleated, the anterior hemisphere was enucleated, the anterior hemisphere was dissected away, excess vitreous humour was removed under dim red light and the eyecup was mounted in a chamber moistened with water saturated wicks and aerated with moistened 95% O_2–5% CO_2. The temperature of the preparation was controlled with a Peltier device.

In the isolated perfused retina, the eye was hemisected, the retina gently removed from the eyecup, and the pigment epithelium was peeled from the retina. The retina was then pinned to a Silgard (no. 184 resin, Dow Corning Corp., Midland, Mich.) dome photoreceptor side up and placed in a Lucite chamber (total volume of 0·7 ml.). All dissections and electrode placement were done under visual control using infra-red image converters. The composition of the oxygenated perfusion solutions is listed in Table 1. The flow rate of the perfusate was 1·5 ml./min.

Electrodes of from 300 to 600 MΩ resistance were made from Pyrex no. 7740

capillary tubing (Corning Glass Works, Corning, N.Y.) on a Livingston type microelectrode puller and filled with 4 M potassium acetate. The electrodes were connected to a negative capacitance preamplifier and all responses were tape recorded for later analysis. Electrodes were advanced through the retina from the vitreal surface in the eyecup preparation and from the scleral surface in the isolated retina preparation.

Toad rod and horizontal cell identification, described in more detail in the text, was based on criteria of response kinetics (Brown & Pinto, 1974), receptive field properties, and spectral sensitivities.

The light source was a tungsten-halogen lamp (General Electric, Quartzline 45W) and the stimulus was a 20 msec pulse of white light. The output of the photostimulator, which had independently controlled test flash and background channels, was focused on the retina so that light spots from 50 to 1200 μm diameters could be shone on the retina.

The test and background intensities were controlled with neutral density filters. Monochromatic lights used in the spectral sensitivity determinations were obtained with narrow band interference filters. The light source was calibrated using a calibrated photodiode (United Detector Technology, Inc., Santa Monica, Model no. 1223). The flux of unattenuated light of wave-lengths between 400 and 700 nm was $0{\cdot}94 \times 10^{-3}$ W/cm^2.

TABLE 1. Composition of oxygenated perfusion solutions (mM)

Perfusate	NaCl	Na_2SO_4	$NaHCO_3$	KCl	$MgSO_4$	$CaCl_2$	Glucose	Tris-HCl (pH 7·8)	Na aspartate
Type I	108	0·6	0·13	2·5	1·2	1·6	5·6	10	0·0
Type II	106	0·6	0·13	2·5	1·2	1·6	5·6	10	2·0

RESULTS

This study describes the responses recorded in eighty-six rods and 105 horizontal cells in the toad which fell into two broad categories, those which behaved as have been previously described in the literature (conventional responses), and those which exhibited periodic variations in membrane potential (oscillatory responses). Both types of responses were observed in the eyecup as well as the isolated retina preparation. Of the cells examined, thirty-six rods and thirty-eight horizontal cells exhibited oscillatory responses which were encountered in two ways. Occasionally oscillations were immediately observed upon impaling a retinal neurone. More usually, conventional responses would be recorded upon impaling the cell. Spontaneously the cell would begin to exhibit oscillatory responses with amplitudes as large as 27 mV in some cells. The oscillations would persist for about 5–15 min when quite spontaneously, conventional responses would once again appear until the cell was lost. In some retinae, only conventional responses were observed, although in these instances the conditions of the experiments were the same as those used when oscillations were recorded. An example of conventional responses in green sensitive rods and horizontal cells is shown in Fig. 1.

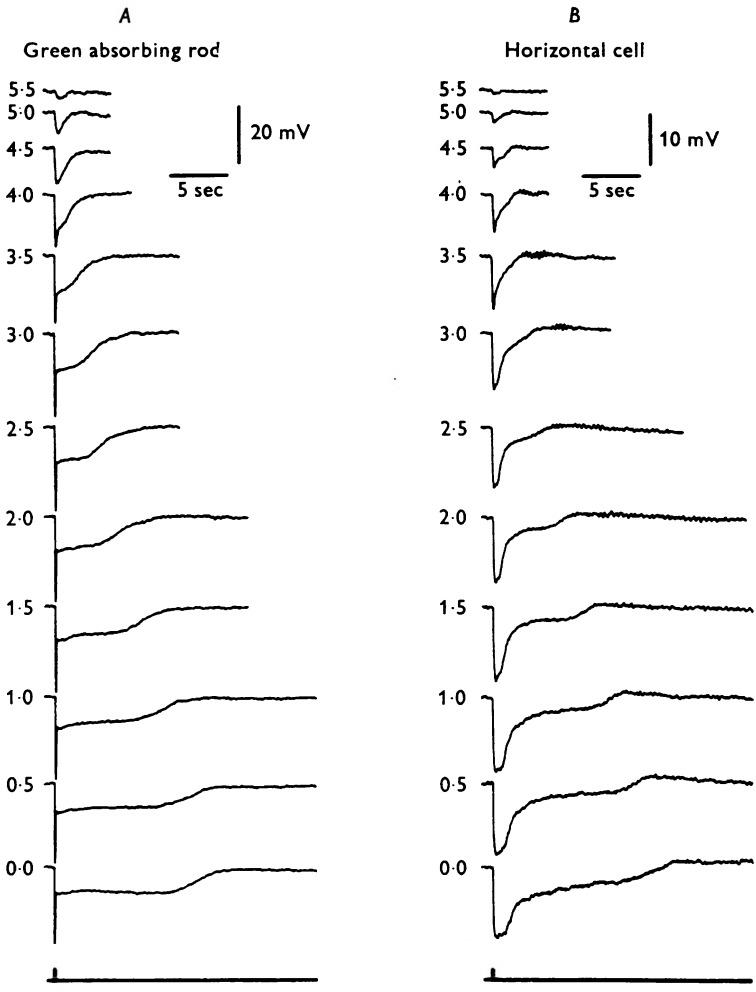


Fig. 1. Conventional intracellular responses to 20 msec white flashes of 1200 μm diameter in the toad retina. *A*, green sensitive rod responses. *B*, horizontal cell responses. In these and in subsequent responses the optical density of the neutral density filter attenuating each flash is shown at the left of each trace. All responses recorded at 25° C with moist 95% O_2–5% CO_2 flowing over retina.

Conventional responses

The most conspicuous feature of the rod response, its large initial transient, was present at brighter test intensities for long (2 sec) and short (20 msec) duration stimuli. Rods show considerable variation in the size of the transient relative to the plateau phase of the response. With

the brightest stimulus, the ratio of plateau to transient amplitude was 0·33 in this cell. In most cells, however, the ratio was between 0·45 and 0·60.

The receptive field properties of the rods were characterized by observing how various diameter spots affected the plots of peak response *vs.* the flash intensity. In most rods, the intensity–response curve measured for a 50 μm diameter spot was translated along the abscissa by 0·6 log units from those curves measured at 100, 200, 400, 800 and 1200 μm diameters, these latter curves all being superimposed.

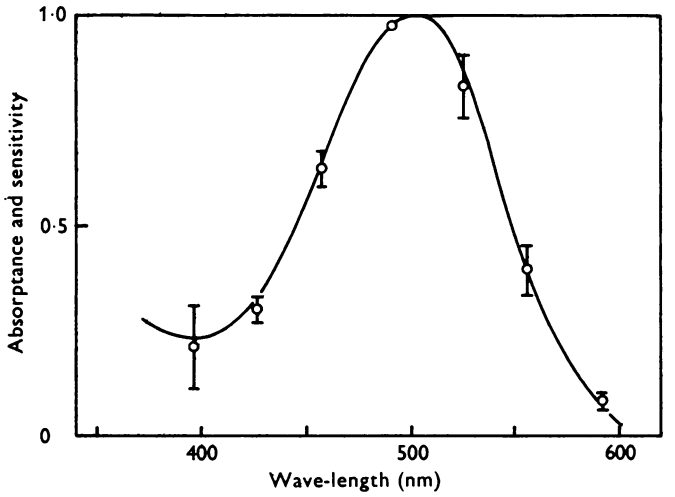


Fig. 2. Comparison of toad rod action spectrum (circles with error bars) and green absorbing rod absorption spectrum (continuous curve, from Harosi, 1975). Action spectrum is the average of spectra measured in five rods; each spectrum has been normalized to absorptance at 492 nm.

All receptor responses were recorded from green sensitive rods as determined by action spectra illustrated in Fig. 2. These were in excellent agreement with the absorption spectrum peaking at 502 nm measured in the *Bufo marinus* green absorbing rod by Harosi (1975). The toad has another rod, the blue absorbing rod, shown by Harosi (1975) to have an absorption peak at 435 nm. Neither blue sensitive rods nor horizontal cells with a prominent 435 nm input were observed in the present study.

The horizontal cell responses shown in Fig. 1*B* exhibit prolonged afterpolarizations similar to those recorded in the rod, suggestive of a large rod input into this cell. When the preparation was light-adapted, horizontal cell responses were faster and did not include a prolonged afterpolarization. Action spectra of light-adapted horizontal cells fit a rhodopsin nomogram peaking around 565 nm, which probably reflects the absorption of the

cone photopigment. Dark-adapted action spectra were considerably broader due to the contribution of rods with a maximum absorption at 502 nm.

The receptive field properties of the horizontal cells fell into two classes. Some cells were characterized by intensity–response curves for various spot diameters which were translated along the abscissa parallel to the 1200 μm diameter curve. This translation of curves was observed with spot diameters increasing to 800 μm. The curves measured with spot diameters between 800 and 1200 μm were all superimposed. For these cells, Riccó's Law was obeyed with excellent fidelity over spot areas varying by a factor of 1000. In the other class of horizontal cells the intensity–response curves measured with smaller spot sizes were translated as before but were also broadened, so they spanned a larger range of test intensities.

Toad rod and horizontal cells behave similarly to the rods and horizontal cells reported in other species (Grabowski, Pinto & Pak, 1972; Schwartz, 1973; Lasansky & Marchiafava, 1974). However, the kinetics of the toad responses are quite slow and, in this sense more closely resemble those of *Necturus* (Fain & Dowling, 1973; Normann & Werblin, 1974). Perhaps the slower toad rod kinetics are important for the development of oscillations.

Oscillations in rods

Oscillations in rod membrane potential were either sustained or transient. Sustained oscillations were present in darkness and were modified by illumination. Transient oscillations of similar frequencies were evoked by light – usually with a long delay – persisted for a few or many cycles and gradually subsided.

An example of sustained oscillations in a green sensitive rod is shown in Fig. 3. The sustained oscillations, temporarily abolished by the test flashes, started again after the rod potential returned to its dark-adapted base line. Sustained oscillations of similar frequency were also recorded in *Necturus* rods, horizontal cells, bipolar cells, and ganglion cells (unpublished observation).

An example of transient oscillations in a green sensitive rod is shown in Fig. 4*A*. With dim flashes, the rod produced conventional responses. Brighter flashes, however, evoked spindles of oscillations which appeared once the rod potential returned to its dark-adapted base line. The amplitude and duration of the oscillations increased for brighter test flashes.

Fig. 4*C* is an expansion in time and voltage of the onset of oscillations in the response to the 0·0 flash shown in Fig. 4*A* and illustrates that rod oscillations were quite constant in frequency and were symmetric about the base line potential. As will be seen later, the horizontal cell oscillations recorded in the eyecup differed in this latter respect.

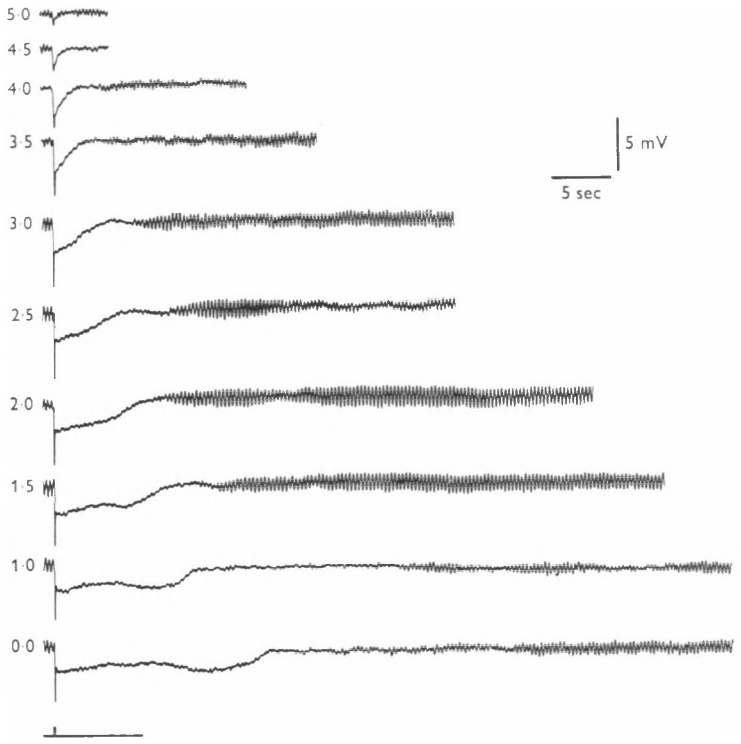


Fig. 3. Sustained oscillations in toad green sensitive rod. Approximately sinusoidal oscillations, present in darkness, are temporarily abolished by illumination. Stimulus was a 20 msec pulse of white light. All responses recorded at 25° C.

Receptive field of rod oscillations

The transient oscillations illustrated in Fig. 4*A* were evoked by flashes illuminating a circle 1200 μm in diameter. Fig. 4*B* shows the responses of the same rod to flashes covering spots of only 50 μm diameter. These responses, recorded immediately after those shown in Fig. 4*A*, were similar to those for 1200 μm spots but the oscillations were absent. As soon as these responses to the 50 μm spots were recorded, a control experiment using 1200 μm diameter spots was performed and oscillating responses were once again observed. Oscillations were increased when the area of illumination was enlarged well beyond the limits which affect the size of the rod hyperpolarization as shown in Fig. 5*A*. The normalized peak response amplitudes of an oscillating rod (open circles) and a horizontal cell (triangles) are plotted versus the spot diameter. The flash

intensity which evoked each response was held constant. Also shown in this plot is the normalized peak amplitude of the transient rod oscillation evoked by illumination of each diameter spot (filled circles). The amplitude of the rod oscillation and the amplitude of the horizontal cell response grow with increasing spot diameters in a very similar manner over spot diameters where the amplitude of the rod light response is constant. This

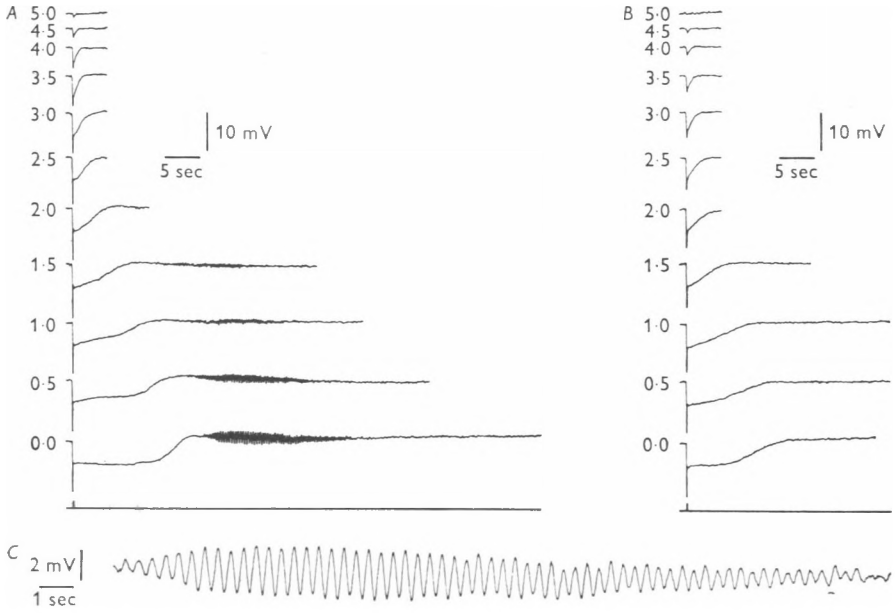
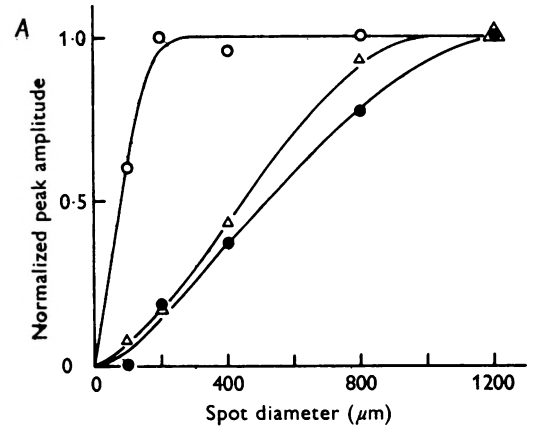


Fig. 4. Transient oscillation in toad green sensitive rod for large and small diameter stimuli of increasing intensities. *A*, light-evoked responses and spindles of oscillations elicited by 1200 μm diameter spot illumination. Note that oscillations are present only after cell potential returns to dark-adapted level. *B*, same rod as in 4*A* but responses were elicited by 50 μm diameter spot. Oscillations here are absent. *C*, an expansion in time and voltage of the onset of oscillations in response to 0·0 flash from 4*A* showing sinusoidal oscillations which were symmetric about the dark potential level. All responses, recorded at 25° C, were to 20 msec stimuli of white light.

observation implies that the rod oscillation is not a phenomenon confined to a single rod but results from an interaction between rods and cells possessing large receptive fields. Similar requirements for large field stimulation to elicit oscillations in the eel optic tract were noted by Adrian & Matthews (1928).

Oscillating rod responses to 400 and 1200 μm diameter spots are superimposed in Fig. 5*B*. The response to the 1200 μm diameter spot returns to

base line more rapidly than the response to the 400 μm diameter spot suggesting that large field illumination may evoke delayed inhibition of rods as seen in the turtle cone system (Baylor *et al.* 1971).



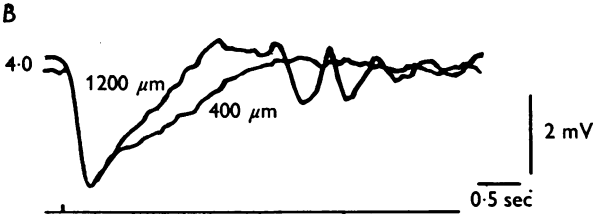


Fig. 5. Receptive field of rod oscillations. *A*, normalized peak amplitudes of rod (open circles), horizontal cell (triangles) and rod oscillations (filled circles) in response to constant intensity (4·0) flash of various diameters. The receptive field of the rod oscillation is more similar to that of the horizontal cell response than that of the rod response. *B*, the peak of two rod responses to 400 and 1200 μm diameter spots have been superimposed. The response to the 1200 μm diameter spot (with oscillations) returns to the base line faster than the response to the 400 μm diameter spot. This suggests that a delayed inhibition with a large receptive field impinges on to oscillating rods. All responses, recorded at 20° C, were to 20 msec stimuli of white light. Test flash was imperfectly centred over electrode causing rod response to 100 μm spot to be smaller than typical.

Horizontal cell oscillations

Horizontal cells, with their receptive fields of approximately 800 μm diameter, might provide the coupling interaction just described. Horizontal cell transient oscillations are shown in Fig. 6. This cell had a large rod input as inferred from the long afterpolarization and the spindles of oscillations similar to those observed in rods. As in rods, these oscillations did not appear until the potential had returned to its dark level.

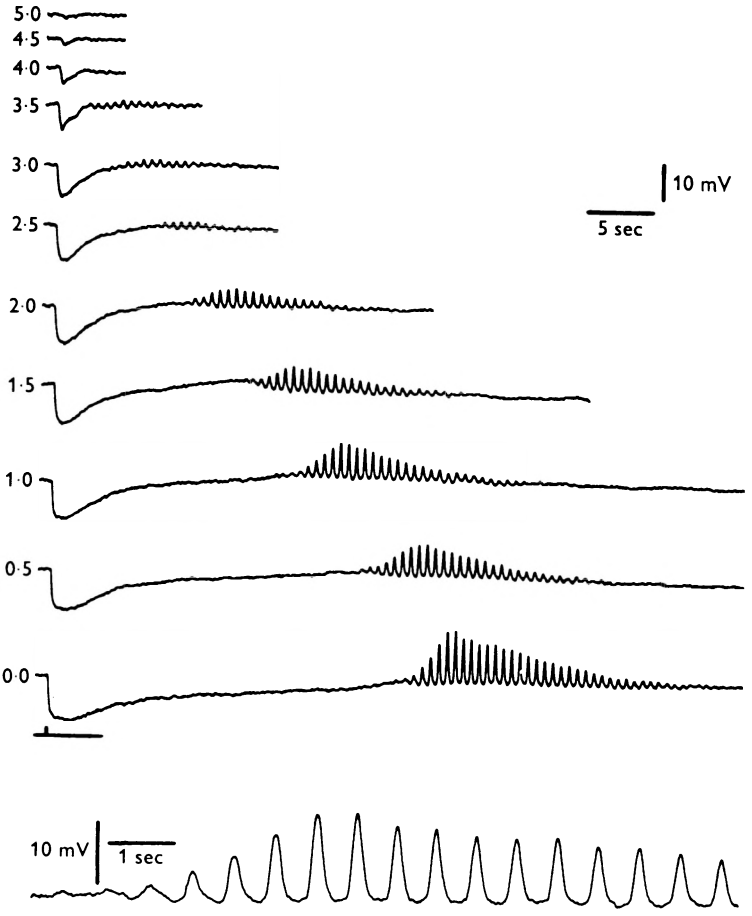


Fig. 6. Transient oscillations in toad horizontal cell. Light-evoked responses and spindles of oscillations elicited by 20 msec flashes of 1200 μm diameter white light. The lower trace is an expansion in time and voltage of the onset of oscillations in response to 0·0 flash and shows 'rectified' oscillations which were asymmetric about the dark potential level. Hyperpolarized oscillating components were absent while only depolarizing components are present. All recordings made at 20° C.

The differences in rod and horizontal cell oscillations are best seen by comparing the lowest trace in Fig. 6 with Fig. 4*C*. In this example, the rod exhibited sinusoidal oscillations but the oscillations of the horizontal cell were 'rectified', presenting large depolarizing and small hyperpolarizing components. This 'rectification' of the horizontal cell oscillations is difficult to explain: it was observed frequently in eyecup preparations but only rarely in the isolated, perfused retina.

Effect of aspartate on rod and horizontal cell oscillations

If the oscillations described above result from an interaction between rods and the large receptive field second order neurones, uncoupling the rods from these neurones should eliminate the oscillations. 2 mM sodium

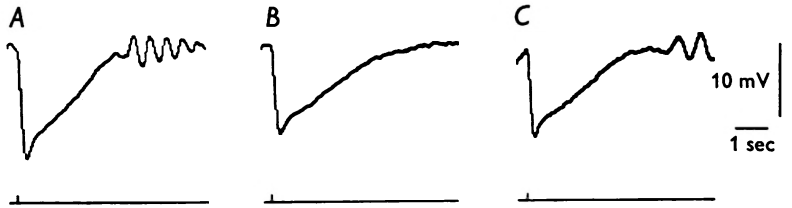


Fig. 7. Effect of aspartate on rod oscillations. A train of large diameter constant intensity flashes was delivered to the retina. Eight responses of an oscillating rod were averaged under each of the following perfusate conditions to eliminate the slight variability from response to response. *A*, type I (normal perfusate). *B*, type II (2 mM aspartate perfusate). *C*, return to Type I (normal perfusate). When normalized, the averaged light responses before and after aspartate were superposable. The response in aspartate returned to base line somewhat more slowly.

aspartate has been shown to isolate toad rods from horizontal cells (Brown & Pinto, 1974) so its effect on the oscillations was studied in the isolated perfused retina. Thirty rods and horizontal cells were studied in the isolated retina, sixteen of which exhibited oscillating behaviour in type I (normal) perfusate. When the perfusate was switched to type II (2 mM aspartate), the light response and the oscillations recorded in horizontal cells were eliminated. In the rods, however, only the oscillation was eliminated. Returning to type I perfusate restored the oscillation in the rods and also restored both the oscillation and the light response in the horizontal cells. The results of this experiment on a particularly stable large amplitude oscillating rod are shown in Fig. 7. When the amplitudes of the responses were normalized, the responses recorded in type II (aspartate) perfusate returned to base line somewhat more slowly than the responses in type I (normal) perfusate. These findings provide further

evidence that the oscillations are generated as a result of rods working in concert with other retinal neurones.

Stability and factors affecting the oscillation frequency

The frequency of the oscillations in rods and horizontal cells was remarkably constant in any one recording. This stability is illustrated in Fig. 8. In a transiently oscillating horizontal cell, the period of each cycle versus the time that the cycle appeared after the onset of oscillations is

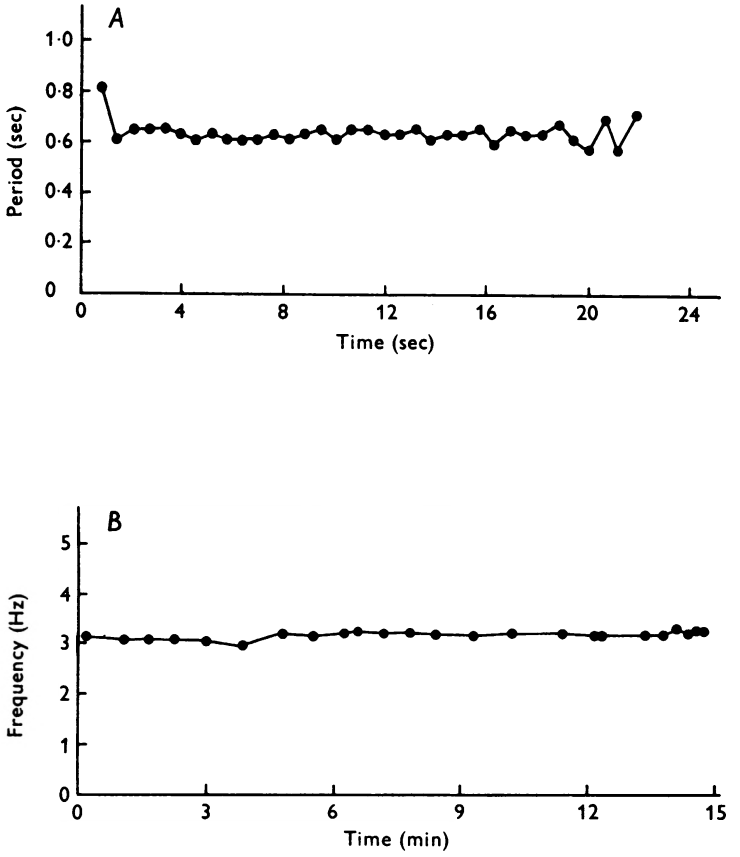


Fig. 8. Stability of oscillation frequency. *A*, period of each cycle *vs.* the time after the onset of oscillations that each period occurred. Data from transient oscillating horizontal cell at 20° C. Average period here is 0·64 ± 0·04 sec. *B*, average frequency of sustained oscillations in a green sensitive rod versus the time after the onset of oscillations. The frequency of the oscillations, averaged over 10 cycles, was measured 24 times during the 15 min the sustained oscillations were observed. Temperature here was 25° C.

plotted in Fig. 8*A*. The average period here was 0·64 sec and the standard deviation of the period was 0·04 sec. In a rod, the average frequency of sustained oscillations, recorded for 15 min before the cell was lost, is shown in Fig. 8*B*.

In any one recording, the frequency of the oscillations could be affected in two ways, by varying temperature and by varying the background illumination. Lowering retinal temperature from 20 to 15° C increased the period of oscillations by a factor of 2. Background illumination significantly reduced the frequency and amplitude of the oscillations. Increasing background intensity by 1 log unit above threshold completely eliminated the oscillations.

A number of experiments were performed attempting to cause a transition from conventional to oscillating responses. Parameters were varied such as retinal temperature over the range of 5 to 35° C, background illumination over a wide range of levels, and oxygen partial pressure. No consistent success was achieved with any of these techniques, although oscillating responses were elicited more frequently at temperatures of 20° C and lower. Adrian & Matthews (1928) reported that application of 0·01 % strychnine to the eel eyecup always caused oscillations in the optic tract activity. This procedure was attempted in the toad retina but, again, without consistent success.

DISCUSSION

Oscillations recorded in rods require either that rods themselves generate this activity or that the oscillations result from interactions with other retinal neurones. The results illustrated in Fig. 3 demonstrated that oscillations were recorded in response to 1200 μm diameter spots but were not elicited by 50 μm diameter spots. The results of Fig. 5*A* show that the rod oscillations grow with increasing areas of stimulation in a manner very similar to the growth of the amplitude of the horizontal cell light response. Since the receptive field for the peak of the rod light response was less than 100 μm in diameter, a rod–rod coupling as described in the turtle retina by Schwartz (1973) cannot account for the large receptive field of the rod oscillations. The rods, therefore, must be coupled to post-synaptic cells with large receptive fields. This interpretation is strengthened by experiments performed in the perfused retina with 2 mM aspartate.

The oscillations may arise as a result of a reverberating interaction, or because the rods simply respond to oscillations generated in the more proximal retinal neurones. Both possibilities necessitate a feed-back system where rods are post- as well as presynaptic neurones. Some evidence for negative feed-back is shown in Fig. 5*B* where the response to large diameter spots returns to base line faster than the response to small diameter

spots. Also, some rod responses recorded in 2 mM aspartate return to base line somewhat slower than the responses recorded in normal perfusate.

Horizontal cells might be the post-synaptic neurones responsible for this coupling and provide a delayed negative feed-back on to rods as they do in the turtle cone system (Baylor *et al.* 1971). Supporting this suggestion is the similarity in size of the receptive fields of the horizontal cell light response and the rod transient oscillation. Further, horizontal cell negative feed-back on to the gecko rod-like photoreceptor has been demonstrated by Pinto & Pak (1974). Thus, a delayed horizontal cell negative feed-back might account both for the origin of the oscillating phenomenon and its large receptive field.

Whether the oscillations are a physiological or pathological phenomenon is a difficult question to answer. Oscillations have been observed in a large number of animals using a wide variety of experimental conditions (Doty & Kimura, 1963). This study described oscillations recorded under two quite different experimental conditions, the eyecup and the isolated retina preparations. It is appropriate to emphasize that the light-evoked responses in both conventional and oscillating modes of behaviour were very similar. The oscillations were an addition to rather than a replacement of the more conventional behaviour. The observations made of the oscillatory state and the conclusions about retinal organization derived from these observations remain pertinent whether the oscillations result from physiological or pathological mechanisms. It is concluded that rod photoreceptors are not autonomous units which work in isolation from their neighbours. Rods can be both post- as well as presynaptic neurones and can be significantly influenced by neighbouring cells which are post-synaptic to the rods themselves.

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